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Climate Warming Shifts Carbon Allocation from Stemwood to Roots in Calcium-Depleted Spruce Forests

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Increased greening of northern forests, measured by the Normalized Difference Vegetation Index (NDVI), has been presented as evidence that a warmer climate has increased both Net Primary Productivity (NPP) and the carbon sink in boreal forests. However, higher production and greener canopies may accompany changes in carbon allocation that favor foliage or fine roots over less decomposable woody biomass. Furthermore, tree core data throughout mid and northern latitudes have revealed a Divergence Problem (DP); a weakening in tree ring responses to warming over the past half century that is receiving increasing attention, but remains poorly understood. Often, the same sites exhibit Trend Inconsistency Phenomenon (TIP), namely positive, or no trends in growing season NDVI where negative trends in tree ring indexes are observed.

Here we studied growth of two Norway spruce (*Picea abies*) stands in western Russia that exhibited both the DP and TIP, but were subject to soil acidification and calcium depletion of differing timing and severity. Our results link the decline in radial growth starting in 1980 to a shift in carbon allocation from wood to roots driven by a combination of two factors: a) soil acidification that depleted calcium and impaired root function, and, b) earlier onset of the growing season that further taxed the root system. The latter change in phenology appears to act as a trigger at both sites to push trees into nutrient limitation as the demand for Ca increased with the longer growing season, thereby causing the shift in carbon allocation.

1. Introduction

During recent decades, climate warming has been pronounced in high latitude circumpolar forests [*IPCC*, 2007]. This trend has been expected to cause an increase in forest growth, and in

fact, a canopy *"greening,"* measured by an increase in the Normalized Difference Vegetation Index (NDVI) occurred during 1982-1998 in high latitude forests [*Myneni et al.*, 1997; *Zhou et al.*, 2001]. More recently, studies of regional trends of growing season NDVI identified some regions in the Northern Hemisphere where summer NDVI seems to have leveled off or declined [*Bunn et al.*, 2007; *Goetz et al.*, 2005; *Zhang et al.*, 2008]. This included central Alaska, where, a "*browning*" trend in NDVI that become visible in the 1990s was explained by temperature induced drought and insect damage [*Verbyla*, 2008]. Averaged over the entire Northern Hemisphere, however, a positive, trend of *growing season* NDVI continued into the 2000-2009 period [*Maosheng and Running*, 2010].

In North America, Europe and Western Siberia, precipitation and temperature increased from 1994-2005, which caused an overall easing of climate growth constraints as shown by Dai et al. [2004], with updates found at http://www.esrl.noaa.gov/psd/. This warming and wetting of the Northern Hemisphere during the last few decades has triggered an earlier start of the growing season (IPCC, 2007), especially in high latitude forests [*Rousti and Heinonen*, 2007; *Vikhamar-Schuler and Hanssen-Bauer*, 2010]. Phenological networks in Europe and North America indicate an average advance of leafing dates from 5 to 20 days [*Menzel and (31)*, 2006].

These changes stand in contrast to dendrochronological records of the last few decades from numerous mid and high latitude regions that show declines in radial growth and weakening in tree responses to temperature variations. These declines in radial growth rate that fail to match expectations have been referred to as the Divergence Problem (DP) (Jacoby and D'Arrigo, 1995; [*Briffa et al.*, 1998; *Jacoby and D'Arrigo*, 1995; *Vaganov et al.*, 1999]. Spruce, dominant trees in many boreal forests, are of particular concern, because they occur in regions where temperature increases are most pronounced. Declines in radial growth are often accompanied by a

weakening of annual tree growth–temperature correlations that are expressed as diverging trends. Therefore, statistical models of tree ring-climate relationships calibrated on pre 1950 to 1970 temperature measurements often underestimate temperature trends of the last few decades. Cook et al. [2004] analyzed chronologies of ring width data, using "north" (high latitudes) and "south" (low latitudes) subsets over 1,000 yr. Both demonstrated reasonable correlations until the appearance of the DP, primarily in the northern subset in recent decades. A number of explanations for the DP have been suggested, including, nonlinear physiologic responses of trees to climate change, pollution effects, and mathematical artifacts of tree ring calibration [*D'Arrigo et al.*, 2008].

In addition to the DP, inconsistencies also occur at the same sites between tree ring indices and trends of growing season NDVI. Inter-annual NDVI variability would be expected to correlate with variations in tree ring indexes. However, the correlation between NDVI and tree rings has been shown to be season dependent, with a positive relationship in summer and a negative relationship in spring [*Kaufmann et al.*, 2008]. Furthermore, our earlier work identified a case of divergence between cumulative growing season NDVI trends and trends of annual ring-width increment [*Lawrence et al.*, 2005]. Recent analysis of decadal trends in growing-season NDVI and tree rings at 22 sites in the Russian and Canadian taiga demonstrate a nearly complete absence of consistency in the direction of these trends [*Berner et al.*, 2011]. No sites with a positive growing-season NDVI trend from1982-2008 showed a positive trend in tree ring increments [*Berner et al.*, 2011]. Thus, in addition to the divergence of tree rings and temperature (DP), there is a *Trends Inconsistency Phenomenon* (TIP) or divergence between tree rings and growing-season cumulative NDVI. Most NDVI-tree ring correlations, however, were derived over relatively short time periods of one to two decades [*Kaufmann et al.*, 2008].

Comparisons of NDVI and tree ring records over 25 years are rare because observations of NDVI can't be extended back to the pre-satellite era. Thus, it is difficult to determine if the cause of the TIP is anthropogenic or an inherited natural feature of forest growth.

There is some evidence, however, that points to a possible connection between the TIP and a recent shift in carbon partitioning in boreal tree species. Analysis of allometric ratios of spruce and other species obtained through destructive analysis at more than 3000 forestry plots in the Russian taiga during 1950-2000 showed trends favoring green parts, and a decline in the share of woody biomass. The same work showed a correlation between changes in allometric ratios and climatic trends [*A.G. Lapenis et al.*, 2005]. Inconsistency between trends in cumulative growing season NDVI and trends in tree ring indices, as well as the DP, have also been linked to stress caused by soil acidification in a western Russian spruce forest [*Lawrence et al.*, 2005].

In the study presented here, we evaluated growth of two Norway spruce (*Picea abies*) stands in western Russia that exhibit both the DP and the TIP. The objective of the study was to determine if changes in climate, phenology, and or soils could lead to a shift in carbon allocation of these trees that would explain the DP and TIP. We utilized climate and NDVI data, tree cores, archived soil samples collected in 1962 and 1964 and additional soil sampling in 2001-2002.

2. Methods.

To conduct this study, data were utilized from two closed canopy forests of Norway spruce in the southern Taiga of western Russia, near St. Petersburg. Both forests provided the unique opportunity to use historic archives of soil samples to measure changes in soil properties over the period of time that overlaps with above-ground observations of climatic variables, tree ring records and satellite measurements. Archived soils collected in 1962 in a protected forest near

the town of Luga, and in 1964 in the research forest of the St. Petersburg Technical Academy of Forestry, near the town of Lisino, were made available with original field notes by the Central Dokuchaev Soil Museum (CDSM), St. Petersburg, Russia. Further details on the Lisino site are available in [*Lawrence et al.*, 2005]. The archived soils were collected and stored as intact profiles of 1-m depth, 25-cm width and 8-cm thickness, in dustproof, wooden boxes, which enabled soil to be removed by depth in a manner that could be precisely duplicated by the modern sampling. The Lisino site has moderately well-drained soil developed from calcareous loess that is relatively enriched in nutrient cations (classified as Podzoluvisols, FAO), whereas the Luga site has well-drained soil that is highly-leached and base-poor (classified as Albeluvisols, FAO). Soils at each site were resampled in 2001 and at a second location (also originally sampled in 1964) within the forest at Lisino in 2002, approximately 5 km from the site sampled in 2001. At each site, a central pit near the location of the archived soil collection was sampled along with additional pits (4 at Lisino site, 3 at the Luga site) located in a radius of 50-100 m from the central pit to establish spatial variability.

Field notes from the 1962 sampling indicated that Luga forest was a mature, 50-70 year old spruce forest without any visible damage from fires or indications past heavy logging. However, the 16 cored trees indicated an uneven-aged stand with a range of tree ages in 1962 (5 trees < 40, 6 trees > 40 but less than 100, 5 trees ≥ 100). Furthermore, our review of 1962-2000 surveys of the same forest quadrangle available through the Committee on Environmental Resources of Leningrad Region, revealed no clear cuts or fires. The Parkovyi quadrangle of Lisino forest where archived and modern soil samples were taken, has a well-documented history of forest surveys starting from the second part of 19th century, which also revealed no clear cuts or fires during the last half of 20th century [*Red'ko*, 1997].

Modern soil samples were air-dried for storage and all samples were passed through a 2 mm sieve before analysis. Percent moisture was determined by drying mineral soil at 100^{o}C, and forest floor samples (Oe/Oa horizons) at 60 ^{o}C. All soil samples were analyzed for pH (deionized water, 1:1 soil: water; Blume et al., 1990), exchangeable acidity and Al (Al quantification limit 0.04 $cmol_c\ kg^{-1}$; H quantification limit 0.02 $cmol_c\ kg^{-1}$;[*Thomas*, 1982]), exchangeable base cations (unbuffered 1N NH_4Cl; quantification limit 0.02 $cmol_c\ kg^{-1}$; [*Blume et al.*, 1990]. Cation exchange capacity (CEC) and base saturation were calculated from the concentrations of exchangeable Ca, Mg, Na, K, Al and H. Organic carbon and nitrogen concentrations were measured on a CN analyzer. Further details of archived/modern soil comparison including assessment of spatial soil variability can be found elsewhere . Concentrations of total lignin and lignin biomarkers in forest floor samples were also measurened in archived and recently collected samples. Because conifer wood is composed only of vanillyl (V) units, whereas fine roots and leaf tissue are composed largely of cinnamyl (C) units [*Otto and Simpson*, 2006], changes in the C-V ratio in the forest floor should reflect changes in production and preservation of wood-derived lignin relative to lignin derived from roots and foliage. Total lignin and lignin biomarkers were extracted from forest floor samples in triplicate using CuO oxidation and quantified by GC-FID (gas chromatography-flame ionisation detector) as described in [*Heim and Schmidt*, 2007].

Daily and monthly temperature, precipitation, and snow cover records were obtained from two weather stations 40 and 70 km from Lisino and Luga, available through the Global Historical Climatology Network of the National Climatic Data Center (http://www.ncdc.noaa.gov). The relationship between Julian Day (JD) of budbreak and Degree Day Sum (DDS) was calculated by a simple linear DDS model with budbreak assigned to a

DDS of 220 above 5°C. The value of 220 was estimated from direct observations of budbreak in 1977 and 1978 in the Lisino experimental forest [*Red'ko*, 1997]. Comparison of this simple linear model with 5 models that accounted for changes in minimum temperature and days with frost [*Hannerz*, 1999] revealed variability in predicted JD values of only a few days. These models also all showed that the increase in JD of budbreak started in the early 1980s, and by 2000, was at least 10 days. There are no direct observations of the date of budbreak in the Luga forest. Because of proximity of the Luga and Lisino forests (about 90 km) we assumed that the JD of budbreak of Norway spruce at these two locations occurs at the same DDS value of 220.

In 2001 and 2002, we collected a single tree core (12 mm diameter) from 47 dominant and codominant Norway spruce trees at the Lisino and Luga sites. A variety of tree sizes were available for coring. Trees > 30 cm diameter at breast height (approximately 1.4 m above ground) were selected to include a range of sizes from trees that were free of visible defects. Annual rings were cross-dated to validate assignment of calendar dates. The climate-tree ring relationships were analyzed according to standard dendrochronological methods [*Cook and Kairiukstis*, 1990].

We used the Global Inventory Modeling and Mapping Studies (GIMMS) data set to derive trends in seasonal and annual NDVI. These NDVI records, which cover 1982 -2006 at ~16 day intervals at spatial resolution of ~8 km, were already corrected for view geometry, volcanic aerosols, and other effects not directly related to vegetation change [*Tucker et al.*, 2005]. For each spruce stand we calculated NDVI for a single 8x8 km pixel centered over soil pits locations, as well as an average of 9 pixels (3x3 pixels) also centered on the soil pit locations. The latter estimate was done to ensure significance of the single pixel estimates. A single pixel NDVI record over 1982-2006 period was considered valid if NDVI values for the

given pixel were within one standard deviation of the 9 pixel averages. The level of statistical significance of this comparison was calculated through a paired t-test of single pixel values with the 9 pixel averages (including the central pixel). GIMMS single pixel data were then used to estimate a mean monthly NDVI value by averaging of the two 16 day measurements closest to the given month. Mean monthly NDVI values were tested for linear trends over the entire 1982 - 2006 period. Statistical significance of the linear trends was estimated through the F-test.

3. Results.

The growing season cumulative NDVI (April-September) estimated for the single pixel showed no significant trends for these two sites from 1982 to 2006. However, summer maximum $NDVI_m$ showed a negative trend ($p<0.05$) (Fig. 1a), and monthly average NDVI showed positive trends ($p<0.05$) in April and September only (Fig. 1b), which were somewhat stronger for the Lisino site than the for the Luga site (Fig. 1b). Because the spruce stands in Lisino and Luga are representative of the forests of the surrounding area, we found a high correlation of seasonal NDVI trends between the central pixel and the average of 9 pixels at each site ($r=0.95$, $p<0.00$ and $r=0.95$, $p<0.05$; for Lisino and Luga, respectively).

Between 1960 and 2006, mean annual air temperature at Lisino and Luga increased 1.5 ^oC (Fig. 2a), but this increase occurred during spring, winter and fall, without an increase in summer (http://www.ncdc.noaa.gov). This pattern of seasonal warming is common in high latitudes [*IPCC*, 2007]. The thickness of snow cover in January and February at both sites declined, which is typical for this region of Russia [*Groisman et al.*, 2006]. Annual precipitation at both locations, however, increased by about 70 mm yr^{-1} or 12% (between 1960 and 2006); increases occurred mostly during late winter-spring and in June. An increase in annual

precipitation is consistent with an overall increase in European Russia of plant available soil moisture from 1958– 1998 [*Robock and Haibin*, 2006]. The Lisino and Luga forests responded to seasonal warming with a 10-15 day advance of budbreak from 1980 to 2000 (Fig. 2).

Despite increasing temperature and precipitation, and a longer growing season, declines in radial growth rate ($p<0.001$), independent of tree age, began at both sites at about 1980; timing that was highly coincident with the decline in JD of budbreak (Fig. 2). Linearly detrended data for 1900-1950 and for 1951-2000 also demonstrated a deterioration of the relationship between radial growth and climate. Overall goodness of fit (adjusted R^2) from stepwise regression between Z-scores and weather variables such as monthly temperature and precipitation ranged from 0.4 - 0.6 for 1900-1950, but 0.01 - 0.28 for 1951-2000.

To evaluate the connection between early budbreak and decline in ring-width increment we split tree ring records into two equal intervals of 50 years, taking into account that radial growth in a given year also is influenced by canopy formed in previous years. In stepwise-forward regressions relating tree ring Z-scores of each year with budbreak date of the corresponding year, and two previous years, no correlations were observed for 1900-1950. However, for corresponding years over the period 1951-2000, a strong correlation was found for Lisino ($r = 0.85$; $p<0.05$) and a somewhat strong correlation was found for Luga ($r = 0.51$, $p<0.1$).

A further connection between early budbreak and decreased radial growth is suggested by a relationship between date of budbreak and growing season maximum NDVI (Fig. 3), which occurs during the period of radial growth [*Zedaker et al.*, 1987]. After removing linear trends from records of $NDVI_{max}$ and JD of budbreak we performed linear regression between these two variables by year and found a strong ($r=0.81$, $p<0.05$), positive relationship for the Lisino site. At

the Luga site this relationship was only marginally significant ($r=0.4$, $p<0.15$), however. Nevertheless, these results indicate an overall statistical connection between the changing phenology and the decline in radial tree growth.

Changes in soil were measured at both sites between the early 1960s and 2001-2002, but these data also indicated that soil at Luga was considerably more acidic in 1962 than soil at Lisino in either 1964 or 2001 (Fig. 4a, Fig. 4b). Nevertheless, the trees at Luga showed the same decline in radial growth starting around 1980 that was observed at Lisino (Fig. 2). These relationships make it difficult to attribute the synchronous growth declines of the two sites solely to increased Ca limitation from soil acidification.

Further analysis of archived soils provided information to suggest a shift in carbon allocation from stemwood to roots or foliage between 1962-1964 and 2001. Total lignin concentration was similar in archived and modern samples, but the ratio of cinnamyl to vanillyl units (C-V ratio) increased approximately 20 % to 40 % at Lisino and 20 % at Luga from the early 1960's to 2001 (Fig. 5). The large increase in the C-V ratio in the forest floor indicates a decrease in production of wood-derived lignin relative to lignin derived from fine roots and possibly foliage. Furthermore, cinnamyl units are less stable in soil than vanillyl units [*Hoffman et al.*, 2009], making the C-V ratio a conservative indicator of a possible shift in carbon allocation from wood to foliage and fine roots.

4. Discussion.

According to the general theory of resource allocation in plants [*Reekie and Bazzaz*, 1987], non-structural carbon compounds are partitioned among essential plant functions to maintain an adequate supply of resources [*Gifford and Evans*, 1981]. For example, if soil nutrient

availability decreases, trees shift carbon to roots to maintain uptake of underground resources [*Gifford and Evans*, 1981; *Lambers et al.*, 2008; *Reekie and Bazzaz*, 1987; *Yanai et al.*, 1998] . In the case of the Lisino and Luga forests, we observed two external factors that could shift carbon partitioning: a) a warmer and wetter climate that advanced the growing season, and b) soil acidification that led to decreased nutrient availability. We hypothesize that these changes in environment caused a shift in carbon allocation away from woody biomass used in radial growth to increased production of non woody tissue such as fine roots and or foliage.

Climate warming increased the growing season, and therefore the opportunity to fix carbon (Wolkovich et al., 2012), but increased annual growth will be achieved only if increases in other requirements for growth can also be met. These requirements include increased uptake of Ca from soil, which, in the case of Luga, is strongly acidified, and in the case of Lisino, has become substantially more acidic between 1964 and 2001-2002.

In the Lawrence et al. paper [2005], radial growth declines and decoupling of the climate-tree ring relationship at Lisino were attributed to acidic deposition, which caused calcium depletion and aluminum mobilization in soils. Other studies in spruce forests have linked soil Ca depletion and elevated Al to increased rates of dark respiration, lower rates of net photosynthesis, increased concentrations of biochemical stress indicators in foliage, increased rates of root turnover and increased accumulation of fine-root necromass [*Godbold et al.*, 2003; *McLaughlin and Wimmer*, 1999; *Minocha et al.*, 1997].

The earlier start of root growth is therefore problematic in these type of soils because the longevity of fine roots is shortened by soil acidification [*Godbold et al.*, 2003]. More replacement of roots damaged by high Al to Ca ratios is needed to maintain a functional root system throughout the extended growing season. In addition, root systems in soils with elevated

Al to Ca ratios also tend to be shallower than those where Ca is readily available [*Godbold et al.*, 2003; *McLaughlin and Wimmer*, 1999], thereby increasing the likelihood of Ca limitation as roots are forced to acquire Ca from a smaller soil volume over an increasing length of time.

These stressed root systems were likely to be further taxed by the trend of increasing spring air temperatures that lead to increased soil temperatures. As soil temperature increases, rates of root respiration and fine-root extension increase, and root longevity decreases, thereby increasing the carbon needed to maintain the root system [*Pregitzer et al.*, 2000]. Although summer air temperatures did not show significant trends, the increase in spring air temperatures results in higher soil temperatures through much of the growing season because the rise in soil temperatures lags behind air temperatures throughout the spring and summer [*Brady and Weil*, 1999].

A shift in carbon allocation from radial growth to fine root growth and maintenance resulting from an earlier onset of spring in combination with lower availability of Ca in soil provides a plausible explanation for the observed weakening of climate-radial growth relationships (the DP) and the inconsistency between the growing season NDVI and radial growth (the TIP). This interpretation is supported by Figure 3, which shows a link between earlier budbreak and a less green, less productive canopy during midsummer when productivity is at its highest. Furthermore, cumulative growing season NDVI showed little or no increase. Without increased production, the increased cost of root maintenance from a lengthening growing season and acidifying soils would require a shift of carbon away from radial growth and canopy maintenance.

The stronger trends of seasonal NDVI values (Fig. 1b) and stronger relationship between radial growth and date of budbreak at the Lisino site than the Luga site may be related to soil

differences. Elevated ratios of Al to Ca at the Luga site were not sufficient to cause a pronounced decline in radial growth before 1962, whereas the start of declining radial growth at the Lisino site did coincide with the chronology of Ca depletion and Al mobilization [*Lawrence et al.*, 2005]. Prior to 1964, the date when Ca depletion was first detected at the Lisino site, high radial growth did coincide with the two most pronounced periods of early budbreak (Fig. 2), suggesting that Ca availability had been previously sufficient to enable growth increases during longer growing seasons. The relatively coarse-textured Luga soils were likely to be naturally more acidic and lower in available Ca than the Lisino soils before the onset of acidic deposition, and didn't show a significant change from 1962 to 2001 (Fig. 4a, Fig. 4b). Therefore the trees at Luga were adapted to a lower availability of Ca, which was reflected in lower radial growth rates ($p < 0.01$) prior to 1960 than the trees at Lisino (Fig. 2). The additional stress on root systems resulting from earlier budbreak during 1980-2000 would be expected to be greater at Lisino than at Luga, because Ca availability at Lisino was decreasing at the same time that the demand for Ca was increasing due to the lengthening growing season.

5. Conclusions.

At the Lisino and Luga forests, the DP and TIP were most likely a reflection of a shift in carbon allocation away from woody biomass. During recent decades, warming at upper latitudes has triggered an earlier start to the growing season in most boreal and northern temperate forests of the northern hemisphere . These changes in forest phenology coincided with increases in annual precipitation over most regions above latitudes of 45-55 ^{o}N, including the northeastern US and Northern and Central Europe [*Dai et al.*, 2004; *IPCC*, 2007]. Furthermore, in much of the same regions, acidic deposition has caused depletion of soil calcium and increased soil Al:Ca ratios

[*Driscoll et al.*, 2001; *A. G. Lapenis et al.*, 2004; *Wright et al.*, 2005]. Therefore, one might expect to find shifts in carbon allocation from stemwood to roots similar to that at Lisino and Luga in wide regions of northern Europe and North America. Because spruce fine roots have a short life span of only few months, and they decompose faster than stem wood debris by at least an order of magnitude [*Levy et al.*, 2004], this shift in allocation towards fine roots could reduce carbon sequestration potential of northern forest soils.

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Figure Captions

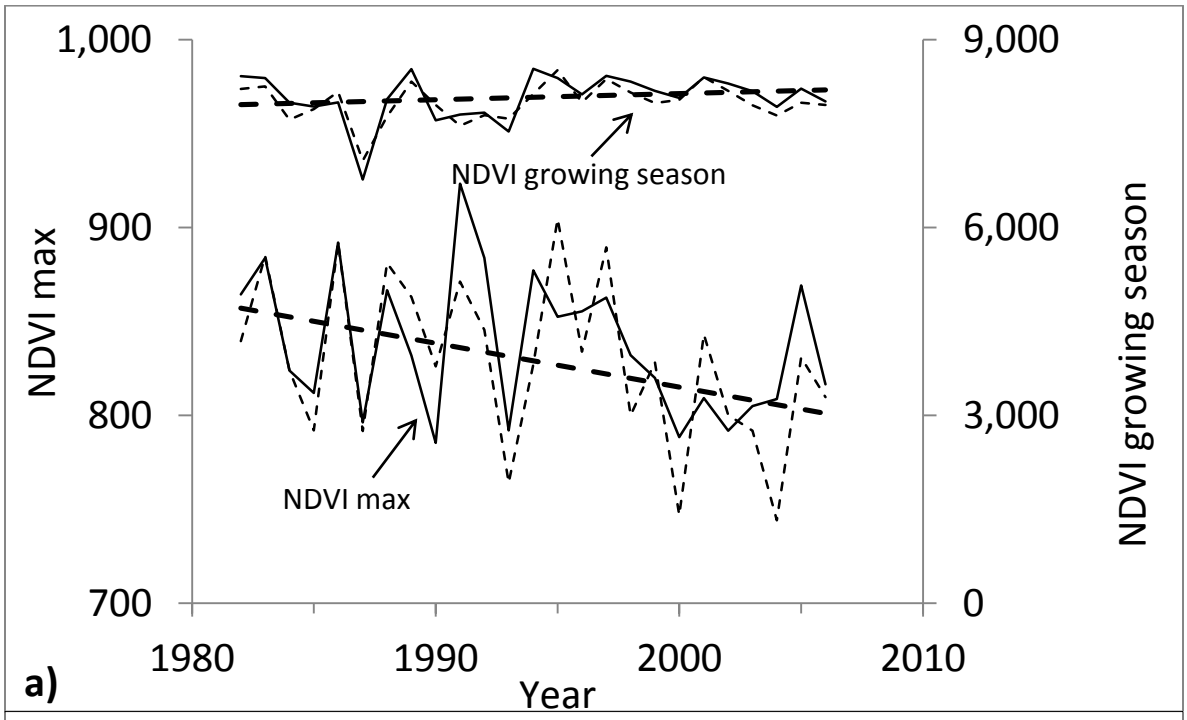
Figure 1. Growing season cumulative NDVI and growing season maximum NDVI ($NDVI_{max}$) for the Lisino (solid line) and Luga (dashed line) sites (a), and linear trends in mean monthly NDVI at Lisino (filled bars) and Luga (open bars), for 24 years of observations (1982-2006) (b). Asterisks indicate significant trends ($p<0.05$). NDVI values are multiplied by 1000 to avoid presenting decimal values less than one.

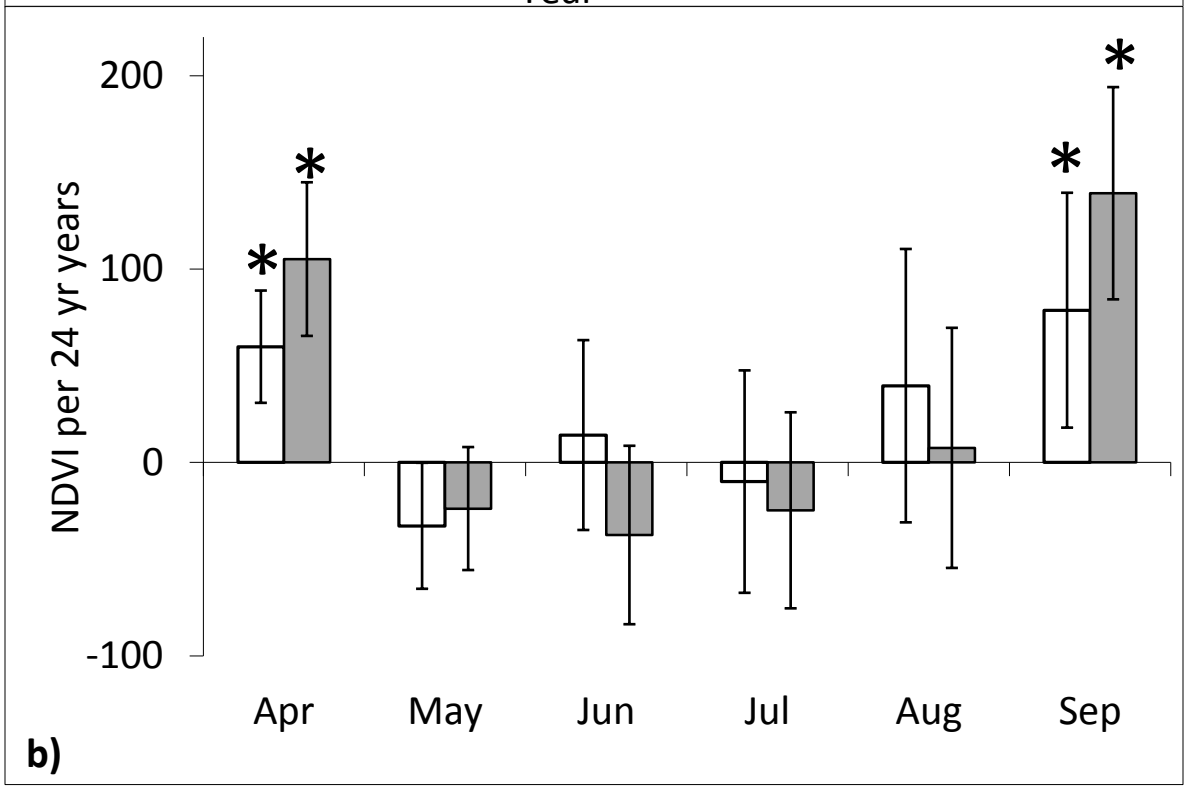
Figure 2. Running three-year average of the Julian Date of budbreak (grey line), and annual Z-Scores of ring-width increment (mean of all tree ages) for the Luga (solid line) and Lisino (dashed line) sites.

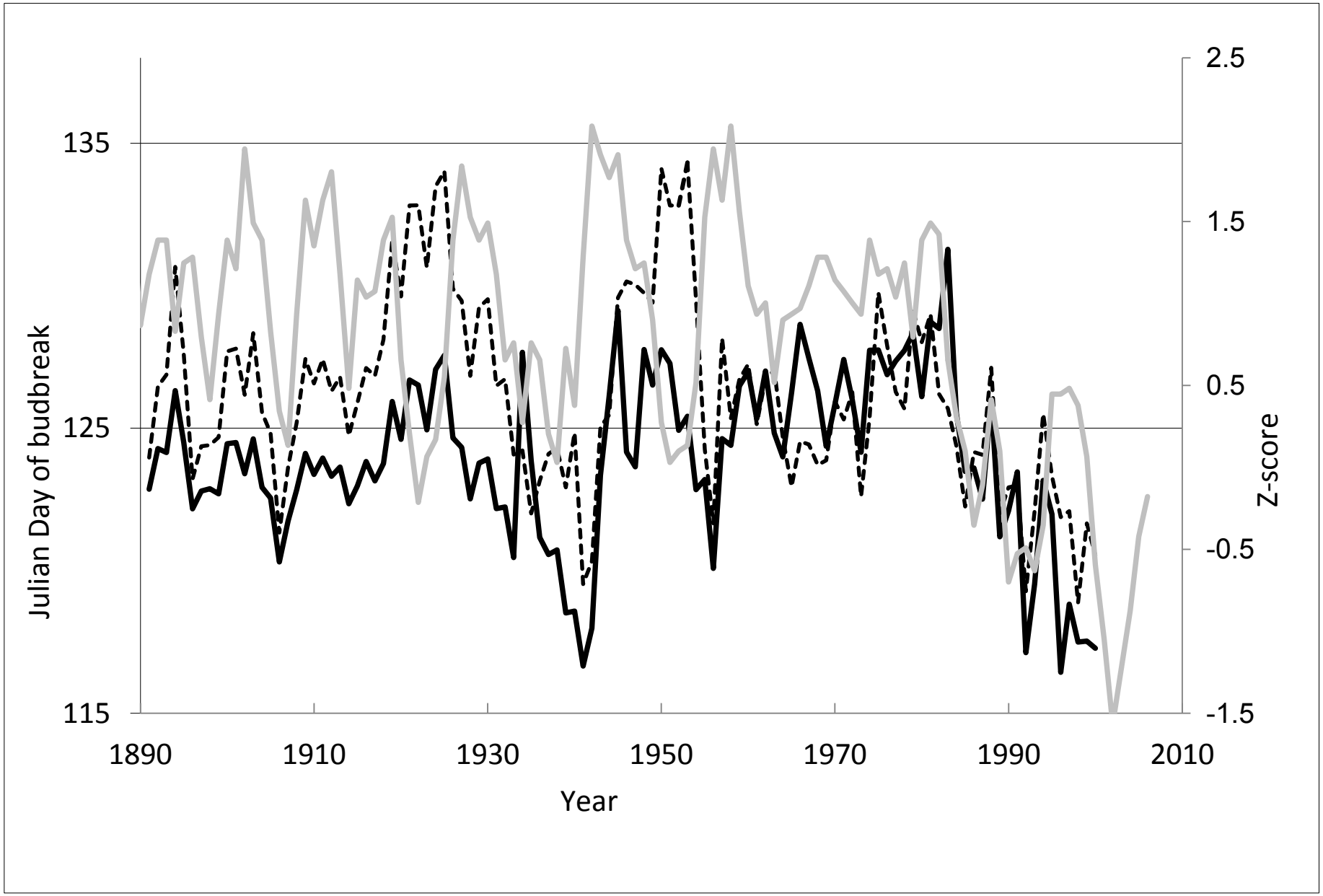
Figure 3. The NDVI growing season maximum ($NDVI_{max}$) that occurs during midsummer (solid line), and Julian Day of budbreak (JD) from 1982 to 2006 at the Lisino site.

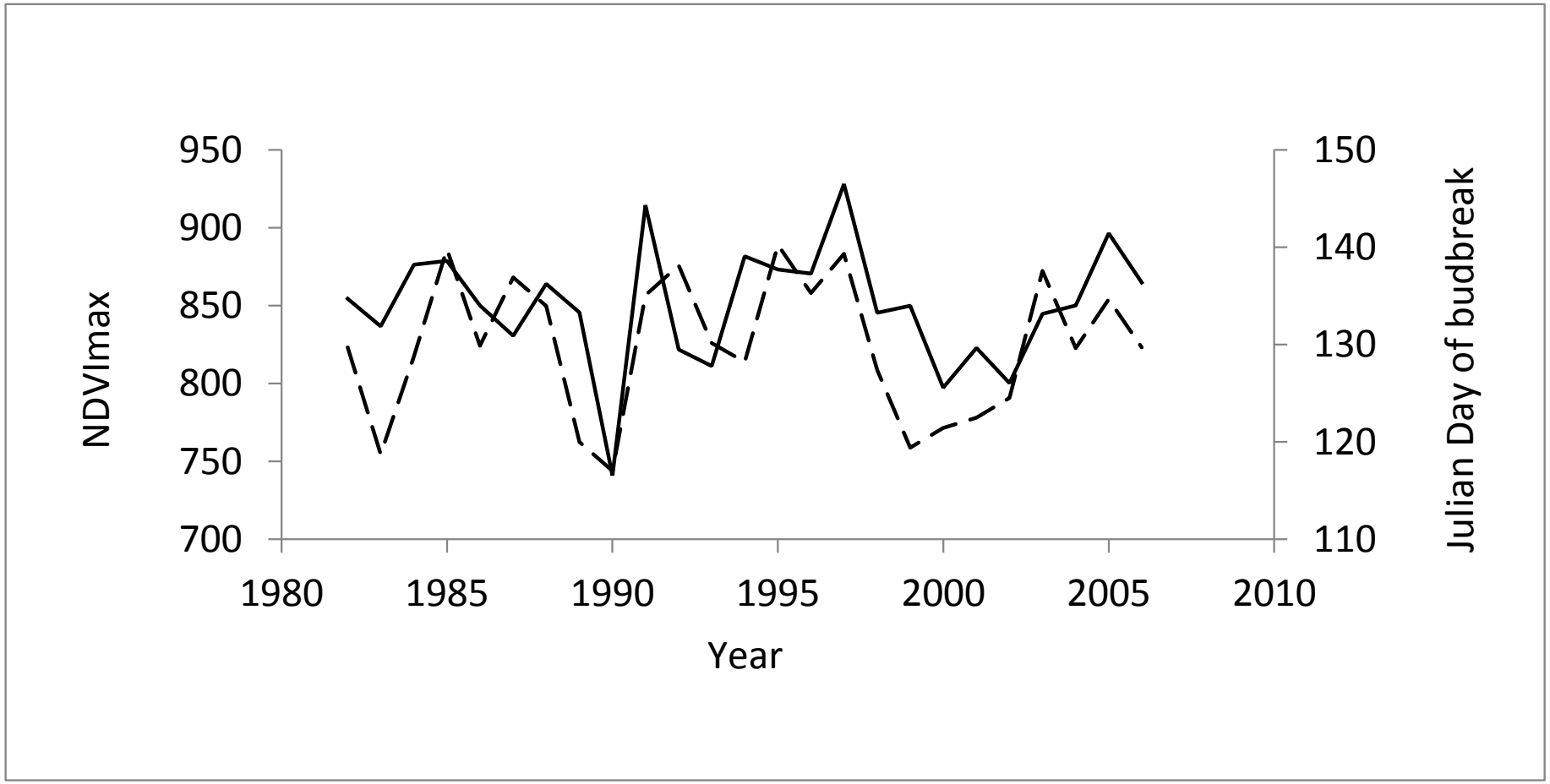
Figure 4. Concentrations of exchangeable calcium (a) and *Al:Ca* ratio (b), in the top 20 cm of mineral soil profiles in 1962 (Luga) or 1964 (Lisino) shown by dark bars, and in 2001 (Luga and Lisino) or 2002 (Lisino) shown by light bars. Error bars indicate spatial variability in the recent sampling.

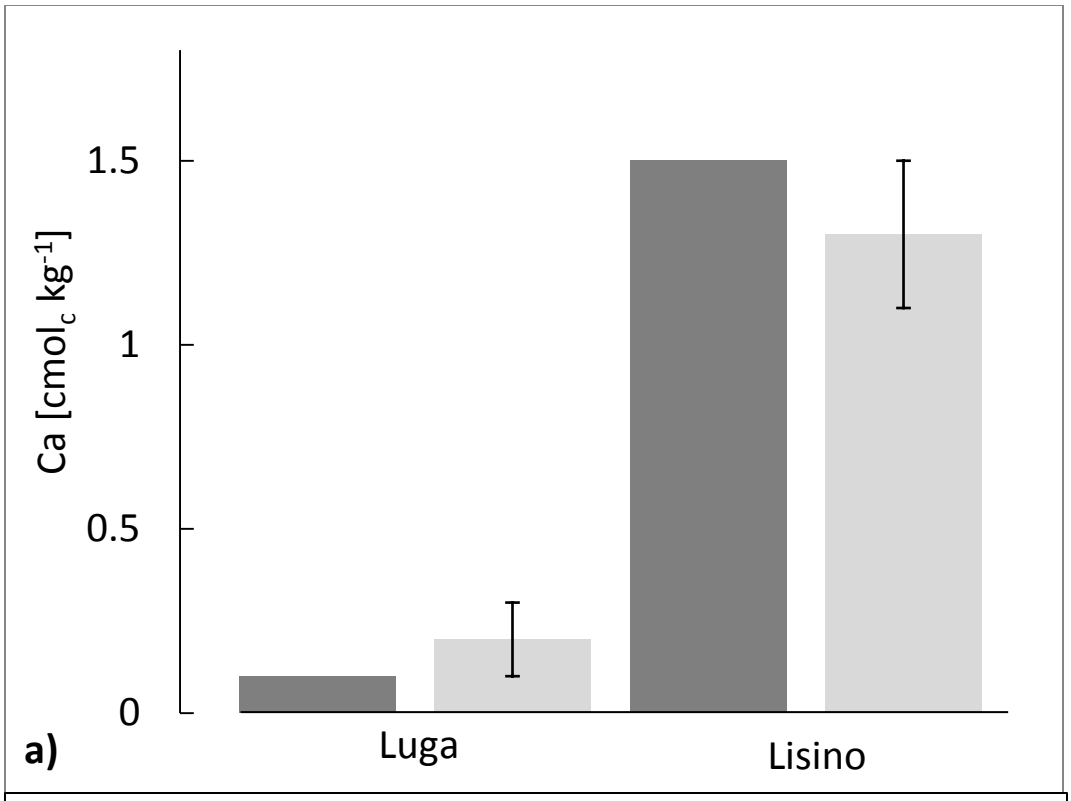
Figure 5. The ratio of cinnamyl to vanillyl units in forest floor samples (Oe/Oa horizons) collected in 1962 (Luga) or 1964 (Lisino) shown by dark bars, and in 2001 (Luga and Lisino) and 2002 (Lisino) shown by light bars. Error bars indicate spatial variability in the recent sampling.

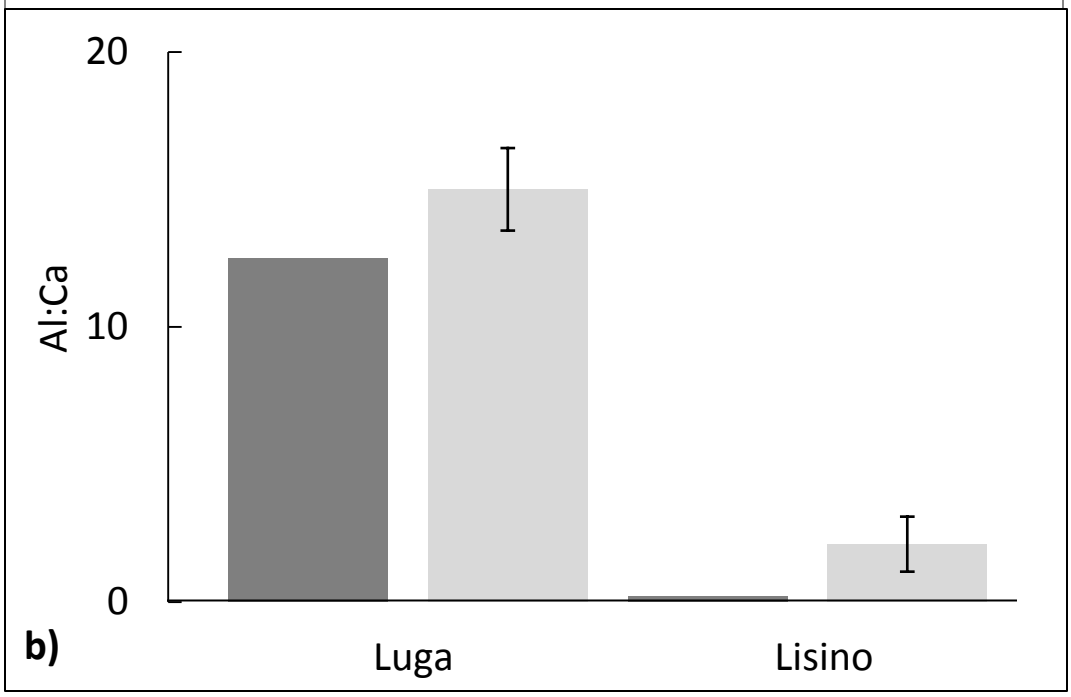

1,000
900
800
700
NDVI max
9,000
6,000
3,000
0
NDVI growing season
NDVI growing season
NDVI max
1980
1990
2000
2010
Year
a)

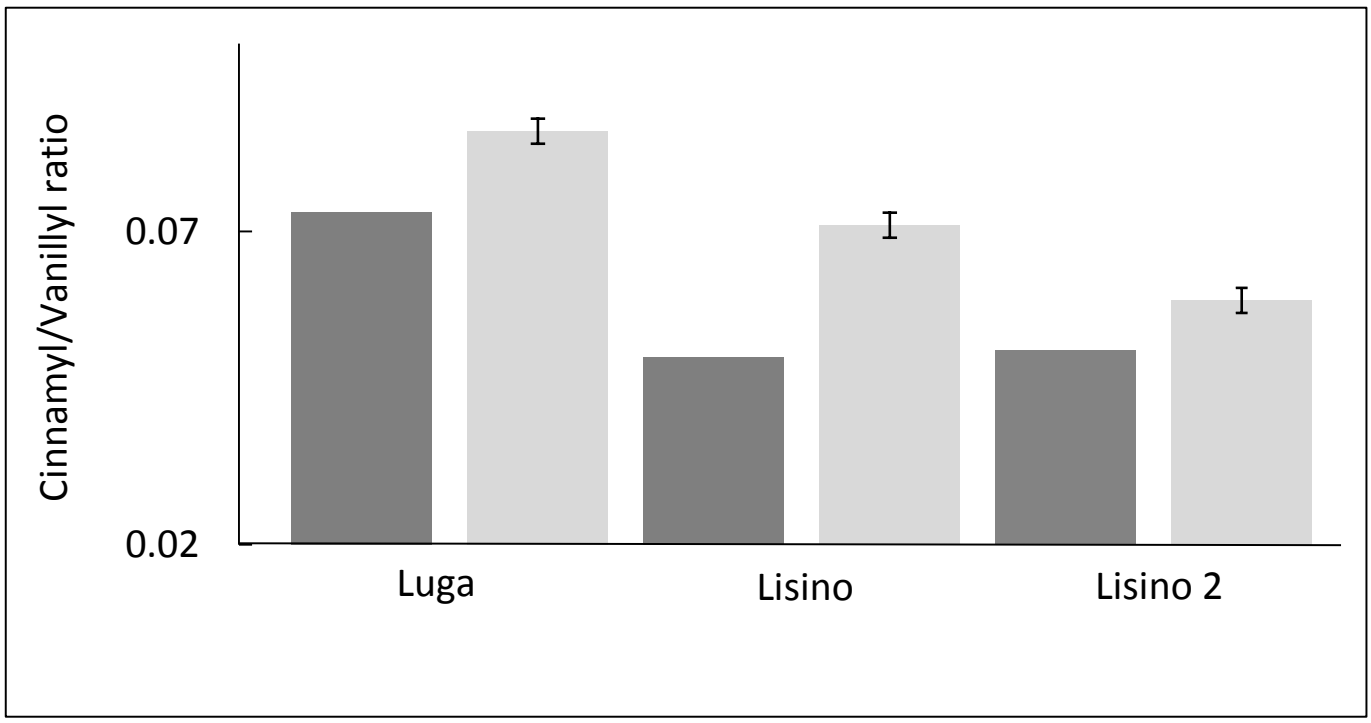

200
100
0
-100
NDVI per 24 yr years
Apr
May
Jun
Jul
Aug
Sep
b)


Julian Day of budbreak
135
125
115
Z-score
2.5
1.5
0.5
-0.5
-1.5
1890
1910
1930
1950
1970
1990
2010
Year


950
900
850
800
750
700
NDVImax
150
140
130
120
110
Julian Day of budbreak
1980
1985
1990
1995
2000
2005
2010
Year


1.5
1
0.5
0
Ca [cmol$_c$ kg^{-1}]
a)
Luga
Lisino


20
10
0
Al:Ca
b)
Luga
Lisino


Cinnamyl/Vanillyl ratio
0.07
0.02
Luga
Lisino
Lisino 2